The most primitive whiteflies (Hemiptera; Aleyrodidae; Bernaeinae subfam. nov.) from the Mesozoic of Asia and Burmese amber, with an overview of Burmese amber hemipterans

D.E. SHCHERBAKOV

Arthropod Laboratory, Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya Str. 123, Moscow 117647, Russia

SYNOPSIS. Relationships, adult morphology, and taxonomic structure of whiteflies are discussed, and their vein nomenclature is corrected. The subfamily Udamoselinae in the broad sense (including Aleurodicinae) is restored; a new subfamily Bernaeinae (family Aleyrodidae) is established comprising most Mesozoic whiteflies. The oldest known whiteflies are described, *Juleyrodes gilli* gen. et sp. nov. and *J. visnyai* sp. nov. from the Late Jurassic (and possibly also Early Cretaceous) of Asia. Their nearest relative, *Burmoselis evelynae* gen. et sp. nov., is from Burmese amber (probably Upper Cretaceous). These genera retain the venation more complete than previously known for whiteflies, confirming that the group descended from Psyllomorpha. Other fossil aleyrodids are listed, as are also the taxa excluded from the group. Burmese amber Hemiptera are reviewed.

INTRODUCTION

Palaeontological evidence supports the classification of Homoptera proposed by Börner (1904) and developed by Hennig (1969) and Schlee (1969), who group whiteflies with psyllids separating them from aphids plus coccids. The fossil record indicates that these two lineages were separate from the very beginning, so, instead of polyphyletic 'Sternorrhyncha', two subordinal names within Hemiptera s.l. are used: Aphidinea (including Aphidomorpha and Coccomorpha) and Psyllinea (including Psyllomorpha and Aleyrodomorpha) (Shcherbakov, 1990).

In contrast, molecular phylogenies of Hemiptera based on 18S rDNA show the whitefly lineage in a variable position (but never as a sister group to psyllids): as a sister group to aphids plus coccids (after separation of psyllid lineage; Campbell *et al.*, 1994; Dohlen & Moran, 1995a: figs. 6–7); as a sister group to all the other Sternorrhyncha (Dohlen & Moran, 1995: fig. 8); as a member of an unresolved tritomy with psyllids and aphids+coccids (Campbell *et al.*, 1995a: fig. 3); or even as a sister group to psocids when the latter are included in the analysis (Dohlen & Moran, 1995: fig. 5). Such a discrepancy could arise from the fact that 18S rDNA in whiteflies is extremely long, with an unusually high substitution rate (Campbell *et al.*, 1994; Dohlen & Moran, 1995), so at present the morphological and fossil evidence should not be discredited simply in favour of novel molecular techniques.

Reduced wing venation of whiteflies has been variously interpreted (Table 1). The two genera described below have an extra vein (free M) which is not known in other genera, their venation being clearly derivable from that of Protopsyllidiidae (Figs. 1, 3, 5). This fact resolves the vein homology and supports a whitefly origin from primitive Psyllomorpha, as concluded already by Quaintance & Baker (1913: 17): 'Aleyrodidae ... form an offshoot from the psyllid stem. This is indicated by the wing venation and by the structure of the mouthparts, legs, and genitalia.' Despite varying tracheal patterns in wingpads, the fossil record shows that the Sc in Hemiptera is always fused to R and R1, often except its base (along basal cell) and its apex (developed as a supernumerary free branch of R1 or R stem)

(Shcherbakov, 1996). The subcostal groove is still traceable along the R+M stem in some protopsyllidiids and whiteflies (Figs. 1, 3, 5). In all extant suborders of Hemiptera the claval veins of the forewing, A1 and A2 (Pcu and A1 in more accurate nomenclature) are primitively united into a Y-vein (ibid.); in primitive Psyllinea it ends near the apex of the clavus, therefore an oblique anal vein joining the posterior margin of the clavus far from its apex in Bernaeinae and Udamoselinae (see below) should correspond to A1, whereas A2 and A1+A2 are incorporated into this margin.

Whitefly wings are usually considered to be uncoupled in flight (e.g. Carver, 1991). Indeed, the hindwing lacks the distal hooks which are present in Cicadinea (=Auchenorrhyncha), psyllids, aphids, and even in vestigial hamulohalteres of male coccids. Nevertheless, it retains a row of about 7–9 strong curved hairs along the proximal C portion (similar to that of psyllids), which aid in keeping the wings together in flight (Quaintance & Baker, 1913: 9). Whiteflies have much higher wingbeat frequencies (143–224 Hz) than other insects with non-fibrillar (synchronous) flight muscles, and the lowest wing loading ever recorded (up to 0.002 g/cm², i.e. lower than in butterflies (Wootton & Newman, 1979; Byrne *et al.*, 1988). Such high frequencies are never reached by insects which have fore- and hindwings operating independently in flight. Partial reduction of interalar coupling in whiteflies could be associated with a unique combination of the high wingbeat frequency and low wing loading, both resulting from their miniaturization.

Aleyrodidae, commonly known as whiteflies and initially considered a single family, were divided into two subfamilies by Enderlein (1909): Udamoselinae, comprising both *Udamoselis* Enderlein and *Aleurodicus* Douglas, and Aleyrodinae. Quaintance & Baker (1913) considered these two genera to be distinct enough to create a third subfamily, Aleurodicinae (leaving Udamoselinae monobasic). Solomon (1935) and Sampson (1943) synonymized Aleurodicinae under Udamoselinae on account of the similar head shape and venation (see Table 2). Schlee (1970) doubted this relationship and now *Udamoselis* is treated as a nomen dubium (as its pupal case and some important imaginal characters are unknown, and the unique holotype male is apparently lost), and Aleurodicinae as a valid subfamily

Table 1   Forewing vein nomenclature in whiteflies according to various authors. The vein symbols used are the usual ones (those from Enderlein and Szelegiewicz are slightly altered for uniformity); cl.f, claval furrow (associated with CuP in Hemiptera); Ax, axillaris (now out of use).

Enderlein 1909	C+R1	Rs	M	–	Cu	A=cl.f	Ax
Quaintance & Baker 1913	C+Sc	R1	Rs	–	M	Cu	A
Börner 1910; Haupt 1934	C	R	M	–	Cu	A	Ax
Gomez-Menor 1944		R	M	–	–	Cu	
Schlee 1970	C	R	M	–	Cu	cl.f	A
Szelegiewicz 1971	C+Sc	R1	Rs	–	M	CuA	CuP
This paper	C	(Sc+)R1*	Rs	M**	CuA	CuP	A***

*   Sc indistinguishably fused to R–R1, not to C (see text).
**   Free M developed only in some Bernaeinae.
***   In fact Pcu (postcubitus = anteriormost anal s.l.; see text).

name (Mound & Halsey, 1978). Some authors have elevated whitefly subfamilies to families and Aleyrodidae *s.l.* to superfamily rank, e.g. Schlee (1970).

As noted by Solomon (1935) and Sampson (1943), the aleurodicine genera *Ceraleurodicus* Hempel (= *Radialeurodicus* Bondar, = *Parudamoselis* Visnya; synonymy after Mound & Halsey, 1978) and *Synaleurodicus* Solomon, and especially *C. kesselyaki* (Visnya, 1941), are strikingly similar to *Udamoselis* in that the paronychium is very thin and hardly detectable, the 3–7th abdominal segments in males possess upper lateral furrows, C is thickened in the male forewing, and in overall venation pattern (except that A is reduced). The anal vein is developed as in *Udamoselis* in some other *Ceraleurodicus* species: *C. splendidus* Hempel and *C. octifer* (Bondar) (Bondar, 1923: figs. 4, 6). In other aleurodicine genera the wing veins show gradual reduction up to only R–Rs left (Sampson, 1943), making it senseless to draw the subfamilial boundary between *Udamoselis* and its nearest relatives. Therefore, despite an incomplete knowledge of the type genus, the name Udamoselinae should be used in the broad sense of Enderlein (1909) and Sampson (1943), i.e. including Aleurodicinae. The abdominal wax plates were recorded in neither *Udamoselis* nor *C. kesselyaki* (perhaps they are reduced or overlooked due to abundant wax powdering in the latter).

In the nymphal characters, *Ceraleurodicus* spp. (including *C. kesselyaki*) are typical Aleurodicinae, except for bearing up to 10 pairs of peripheral intersegmental ridges, at least several of them with tracheal ducts (instead of 3 tracheal ducts, paired thoracic and unpaired caudal, as usual; Sampson & Drews, 1957; Gill, 1990). Such ridges are found elsewhere only in *Bondaria* Sampson & Drews (imago unknown; Sampson, 1943), and imply a more complete complement of spiracles than the usual 4 pairs (2 thoracic and 2 abdominal); this supposedly primitive character merits reexamination. If the nymph of *Udamoselis* (when discovered) also bears the dorsal ridges, it would be possible to subdivide Udamoselinae into two tribes, a nominate one (including *Ceraleurodicus* and *Bondaria*) with ridges, and Aleurodicini without them.
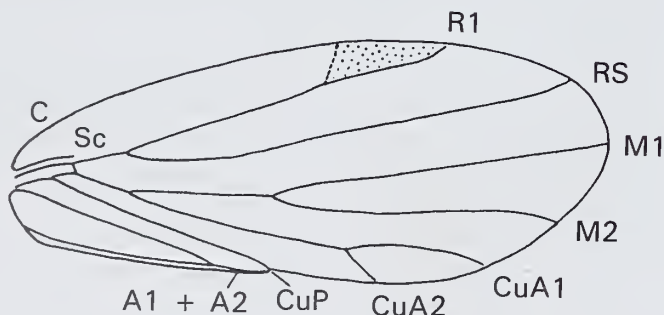
Fig. 1   *Cicadellopsis* sp. (Protopsyllidiidae), PIN 1255/410, forewing venation; Middle Jurassic; Yenisei River near Krasnoyarsk (Kubekovo locality).

Table 2   *Udamoselis* compared to Alerodicinae and Aleyrodinae in the characters of imago diagnostic at subfamily level.

	Udamoselis	Aleurodicinae	Aleyrodinae
paronychium (empodium)	not visible	spine-like	blade-like*
abdomin. wax plates: male	not describ.	3–5th segs.	3–6th(–4th)
abdomin. wax plates: female	?	3–6th segs.	3–4th segs.**
forewing C	thickened	thick./not	not
CuA	present	present/lost	vestigial/lost
forewing CuP	present	present/lost	present
forewing A	oblique	oblique/no	longitud?/no
vertex	conical	conical/not	not

*   In *Siphoninus* Silvestri one claw rather than paronychium is absent (Gomez-Menor, 1944).
**   Segmental origin of two wax plates in female Aleyrodinae was variously interpreted: 4th & 5th segments (Bemis, 1904: fig. 42), 3+4th & 5+6th segments (Haupt, 1934; Weber, 1935), or 3rd & 4th (Gill, 1990: fig. 2.13); the latter version is adopted here as consistent with a sexually monomorphic condition in *Neomaskellia* Quaintance & Baker.

The oldest whitefly imagines known so far, *Bernaea neocomica* (single female) and *Heidea cretacica* (single male), were described from Lower Cretaceous Lebanese amber by Schlee (1970). He mentioned several symplesiomorphies (head broad; eyes not subdivided; median ocellus retained; antennae 8-segmented; paronychium broad; abdominal wax plates absent; male parameres held vertically; ovipositor long, horizontal) and only one doubtful synapomorphy (rostrum reaching beyond hind coxae) of Cretaceous genera relative to Cenozoic whiteflies. Being an orthodox cladist, Schlee created no suprageneric taxon for these two genera. Later, Zherikhin (1980: 51, 80) introduced a family name for them, separating Bernaeidae from Aleyrodidae (all other whiteflies); however, Bernaeidae published in the chronological table without reference to any characters is a *nomen nudum* (ICZN Article 13e).

Living whiteflies are unusual among insects in that their taxonomy is based on the immatures, and not on imagines which are generally neglected and imperfectly known. Schlee underestimated the structural plasticity of Aleyrodidae; in fact, some bernaeid characters still persist in several extant genera. These data, along with information on new bernaeid taxa from the Late Mesozoic of Asia, Burmese amber (all described below), and Lebanese amber (D. Shcherbakov & D. Azar, pers. comm.), allow the revision of the diagnosis and rank of the group.

The diagnostic characters of bernaeids are discussed consecutively:

1.   Relative head width is variable: the head is generally narrow in Udamoselinae, but sometimes 0.85 as wide as the thorax in Aleyrodinae (as in some species of *Aleyrodes* Latreille: Gomez-Menor, 1944: fig. 3); the remaining difference could be attributed to the better developed and more globose eyes in bernaeids; two bernaeid genera described below have a narrow head.

2. Degree of separation between the upper and lower eye parts in Aleyrodidae varies from total to almost none (e.g. in *Ceraleurodicus splendidus*; Bondar, 1923: fig. 4).

3. The median ocellus is retained in *Paraleyrodes* (Gill, 1990) and possibly also in *Aleurodicus destructor* (R.J. Gill, pers. comm.); it is either small or lost in some undescribed Lebanese bernaeids.

4. 8-segmented antennae are recorded in *Aleurodicus destructor* from Thailand (R.J. Gill, pers. comm.); in bernaeids antennae are usually 11-, sometimes 10-, 8-, and even 5(?)-segmented.

5. Paronychium (empodium) is broad, spatulate, longer than claws in *Aleurochiton* Tullgren (*s. s.*; Sampson, 1943); microscopic paronychium is invisible in compression fossils, and in the amber bernaeids its shape could vary from leg to leg, depending on preservation (see Schlee, 1970: fig. 16).

6. In modern whiteflies the wax produced by the abdominal plates is distributed over the body with all three pairs of tibiae possessing specialized setation (Navone, 1987; Byrne & Hadley, 1988). In *Bernaea* the setal combs on the mid and hind tibia (see Schlee, 1970: fig. 16) appear very similar to those of the present-day whiteflies (R.J. Gill, pers. comm.). In various undescribed bernaeids from Lebanese amber the setal rows on tibiae are also somewhat differentiated, and, moreover, the plates themselves are sometimes observable as well. One could assume that the wax-secreting areas on the abdominal venter (perhaps initially not as clear-cut plates) along with complex waxing behaviour were already acquired by the first (Jurassic) aleyrodoids.

7. Parameres are held horizontally in Aleyrodidae, but those of *Bemisia* Quaintance & Baker turn upward at a rather abrupt angle (R.J. Gill, pers. comm.).

8, 9. Both ovipositor and rostrum are extremely long in *Aleurotithius* Quaintance & Baker, allowing it to feed and oviposit on its host plant which is covered with very dense, long hairs (Quaintance & Baker, 1914). This long ovipositor, as well as the normal, short whitefly ovipositor (Weber, 1935: figs. 37–38), has changeable orientation: folded upwards at rest, moving posteriorly when in use. An outline of abdominal apex in *Bernaea* implies that its 'horizontal' ovipositor (directed posteriorly) was already capable of moving upwards, its tip fitting just beneath the modified anal tube (Schlee, 1970: figs. 14, 15; the tube homologized with fused 8–10th tergites (after Weber, 1935), but at least in *Bernaea* the 8th tergite is still free (fig. 15)). The rostrum is of variable length in bernaeids, either just reaching, or extending beyond, the hind coxae (the former condition being quite similar to the typical aleyrodid one).

10. Finally, the forewing venation of bernaeids is even more diverse than the aleyrodid one: from the most complete version known for Aleyrodomorpha, towards reduction of M and A, then of R1 and CuA (thus only R–Rs and claval furrow left), up to a nearly veinless wing blade in *Heidea* (see Schlee, 1970: figs. 3, 6, 7). It is noteworthy that the reduction trend is the same as across living Aleyrodidae, from *Udamoselis* to typical Aleyrodinae. Hindwing CuA seems to be always developed in bernaeids.

A few other characters show somewhat different distribution in bernaeids than in other whiteflies. A coronal suture is retained in most bernaeids (not recorded in *Bernaea* and *Heidea*), and lost in aleyrodids. R1 originates before the forewing midlength in bernaeids, and usually beyond it in Aleyrodidae. The basitarsus is usually longer than the distitarsus in bernaeids, and usually subequal to it in aleyrodids.

Therefore, neither venation nor body structure (possibly except male genitalia) are reliable in discriminating between bernaeids and typical whiteflies, most characters demonstrating intergradation. Moreover, the earliest member of Udamoselinae from Lebanese amber (D. Shcherbakov & D. Azar, pers. obs.) shows, along with the male genitalia and venation typical of the subfamily, such bernaeid features as wide head, rounded eyes, and long rostrum.

No one bernaeid character state could be regarded as apomorphic (including a long rostrum: in Mesozoic homopterans rostra are commonly longer than in their living descendants), so this group is paraphyletic relative to extant whiteflies. Bernaeids are more similar to Udamoselinae, e.g. in the forewing C often thickened, and wax plates on 3–6th abdominal segments in the female. In turn, Udamoselinae are ancestral to Aleyrodinae (Bondar, 1923: fig. 1) rather than constituting its sister group (Campbell *et al.*, 1995b). Instead of separating Bernaeidae from all other whiteflies, it seems reasonable to treat them as a taxon of the same rank as Udamoselinae (=Aleurodicinae) and Aleyrodinae, i.e. as a third subfamily of Aleyrodidae *s.l.*, or, alternatively, as one of three families within Aleyrodoidea (the former opinion is accepted herein).

SYSTEMATIC DESCRIPTIONS

The material described is in the collections of the Department of Palaeontology, The Natural History Museum, London (register numbers with the prefix In.), and in the Palaeontological Institute, Russian Academy of Sciences, Moscow (register numbers with the prefix PIN).

Family **ALEYRODIDAE** Westwood, 1840
Subfamily **BERNAEINAE** subfam. nov.
[Bernaeidae Zherikhin, 1980: 80, *nomen nudum*]

DIAGNOSIS. Imago. Head usually as wide as thorax, with coronal suture. Eyes entire, rounded. Median ocellus usually retained. Antennae (5)8–11-segmented. Forewing with convex R–R1 (R1 separating before wing midlength), concave Rs, faint concave M, convex CuA, concave claval furrow (CuP), and oblique convex A; C often thickened; M often, and sometimes also CuA or nearly all veins, reduced. Rostrum reaching at least hind coxae. Basitarsus usually longer than distitarsus. Paronychium broad. Wax plates on 3–6(7?)th abdominal segments in female. Male parameres held vertically. Ovipositor relatively long.

COMPOSITION. 4 genera (plus several undescribed ones), Upper Jurassic to Cretaceous (?and Paleogene) of Asia.

REMARKS. In two other, extant subfamilies: head narrower than thorax, without coronal suture; eyes subdivided into the dorsal and ventral part (or at least anteriorly emarginate); median ocellus usually absent; antennae 3–7(8)-segmented; forewing lacking M, with R1 origin usually beyond midlength; rostrum usually shorter; basi- and distitarsus usually subequal; paronychium usually blade- or spine-like, or reduced; parameres held rather horizontally; ovipositor usually short. In Aleyrodinae, C is never thickened, and wax plates on 3–4th abdominal segments in female.

In *Bernaea neocomica* the anal vein seems to be developed like in *Ceraleurodicus bakeri* (Bondar) (Bondar, 1923: fig. 8), i.e. oblique and very close to the forewing base, as could be deduced from Schlee's (1970) fig. 25. The impression fossils of Bernaeinae are often preserved with the anterodistal segment of the forewings folded back.

Genus *JULEYRODES* gen. nov.

TYPE SPECIES.   *Juleyrodes gilli* sp. nov.; Upper Jurassic or Lower Cretaceous; Mongolia.

NAME.   From the Jurassic and the genus *Aleyrodes*.

DESCRIPTION.   Forewing widened towards shallowly rounded apical margin. Costal margin markedly arched and thickened (especially near base). Rs 3–4 times longer than R stem. Complete M developed basad of R1 origin (about 1/3 of wing length) and joining CuA basally, nearer to CuA distally. Anal vein occupying 1/2 of clavus. Head narrower than thorax. Antennal flagellum slender.

OTHER SPECIES.   *J. visnyai* sp. nov., Late Jurassic of Kazakhstan.

REMARKS.   Distinct in complete M, short R stem, long A, and forewing shape.

Juleyrodes gilli sp. nov.   Figs. 2–5

HOLOTYPE.   PIN 4307/231, right forewing (part and counterpart; costal margin incomplete); central Mongolia, Ara-Hangayn aymag, 6 km W of Hotont somon, northern part of Uhaa Mt. (Hotont locality, outcrop 354/7); Upper Jurassic or Lower Cretaceous.

NAME.   After Dr R.J. Gill, an expert in living whiteflies.

DESCRIPTION.   Forewing about twice longer than wide, gradually widening towards an obliquely and shallowly rounded apical margin.

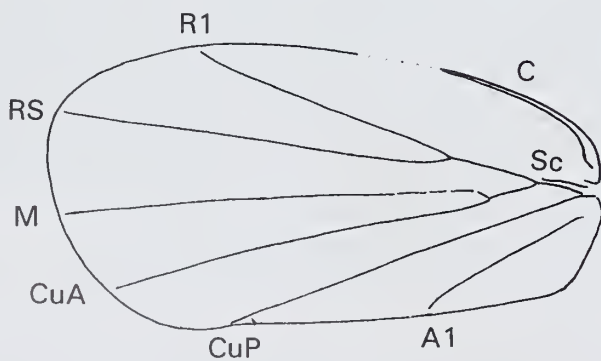Fig. 2   *Juleyrodes gilli* sp. nov., holotype forewing PIN 4307/231, Hotont.

Fig. 3   *Juleyrodes gilli* sp. nov., holotype (venation).
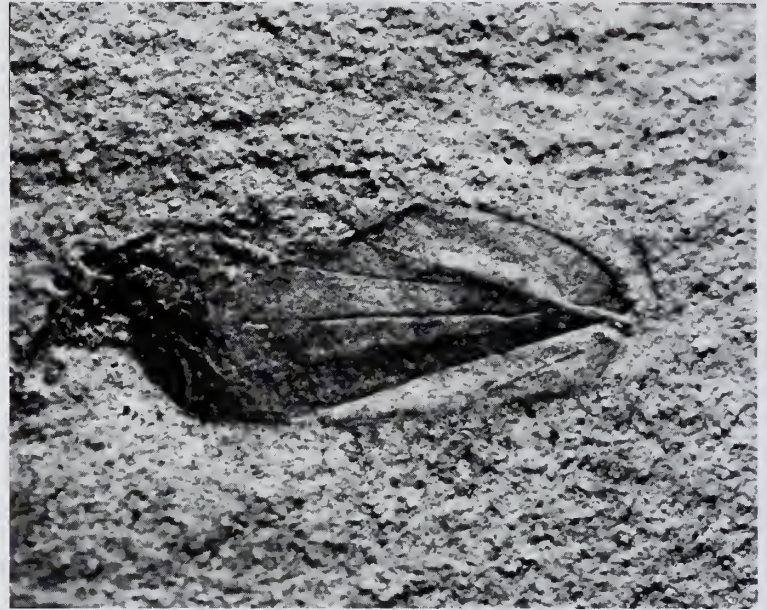

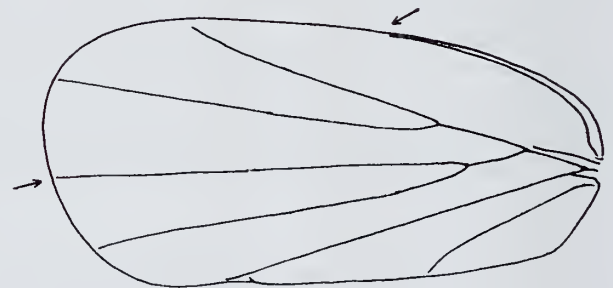Fig. 4   *Juleyrodes ?gilli* sp. nov., forewing PIN 3965/445, Hutel-Hara.

Fig. 5   *Juleyrodes ?gilli* sp. nov. (venation); the wing segment folded back in the impression (arrows) shown in natural position.

Costal margin markedly arched and thickened proximally, more so towards base. R stem straight, raised. R1 longitudinal, 2.6 times longer than R stem, originating at 0.3 wing length, convex and subparallel to C proximally, faint distally, ending well beyond Rs midlength. Rs as fine groove, about 4 times as long as R stem. M clearly joining CuA, continued basad as a groove along M+CuA fusion (which is half as long as the R stem), proximally as unpigmented groove, distally as faint vein nearer to CuA. CuA as faint convex vein, A as fine convex one (turning faint distally). Clavus occupying about 2/3 of wing length; anal vein rather long, 1/2 of clavus (nearly 1/3 of wing length). Forewing dusky, more so along C and R stem, and in clavus, with dark veins (especially C, R, and A).

MEASUREMENTS.   Forewing: length, 2.1 mm; width, 1.1 mm (holotype).

MATERIAL.   Specimen PIN 3965/445, left forewing (part and counterpart; anterodistal wing segment folded back); eastern Mongolia, East-Gobi aymag, 70 km SW of Saynshand somon, eastern Hara-Hutul Range (Hutel-Hara locality, outcrop 300); Upper Jurassic or Lower Cretaceous, lower Tsagaan Tsav Formation. The specimen differing from the holotype in the slightly more elongate wing could represent either another sex of the same species, or one more, closely related species; more pronounced wing relief and less obvious pigmentation are attributable to somewhat different character of preservation.

Juleyrodes visnyai sp. nov. Figs. 6, 7

HOLOTYPE. PIN 2997/3837, complete female? (part and counterpart); southern Kazakhstan, Karatau Range, Mikhailovka; Upper Jurassic, Karabastau Formation; the only specimen.

NAME. After Dr A. Visnya, a discoverer of *Ceraleurodicus kesselyaki*.

DESCRIPTION. Forewing with apical margin shallowly rounded. Costal margin strongly arched and thickened proximally, even more so towards base. R stem arched, continued with Rs. R1 oblique, 1.8 times longer than R stem, originating at 0.33 wing length, markedly converging with C, ending before Rs midlength. Rs 3.3 times longer than R stem. M poorly traceable (as a groove along M+CuA and distally nearer to CuA). Forewing dusky, with dark veins. Hindwing more transparent, with dark veins, distinct R1 originating distally. Body squat. Head 3/4 as wide as the mesothorax, with anterior margin produced rounded trapezoidal between eyes. Antennal flagellum slender, multisegmented. Legs untraceable. Abdomen terminating in two rounded lateral lobes, and dorsomedian projection (anal tube); beyond the latter only traces of presumed ovipositor are visible (on positive impression).

MEASUREMENTS. Forewing length, 3.2 mm; body length (excluding ovipositor), 3.0 mm; antenna length, 0.9 mm; head width, 0.7 mm; mesothorax width, 0.95 mm.

REMARKS. Distinct from the type species in the larger size, broader costal area, arched R stem, and shorter, oblique R1. From the same locality, two more whitefly specimens are known, less completely preserved, and smaller in size than *J. visnyai* holotype (female?). Both have the head narrower than the thorax, and are presumably males. PIN 2997/5071 (body 2.05 mm, forewing 2.2 mm long) is attributable to the genus *Juleyrodes* on account of its markedly arched and thickened C; despite dissimilar head shape (Fig. 8), it could even turn out to be a male of *J. visnyai* (however, sexual dimorphism is not widespread in whiteflies, e.g. in *Ceraleurodicus kesselyaki*, where the male, bearing very long parameres, is larger than female). PIN 2239/532 (body and forewing length 2.3 mm) with less arched C could be identified only as Bernaeinae gen. indet., possibly related to one of two narrow-headed genera described
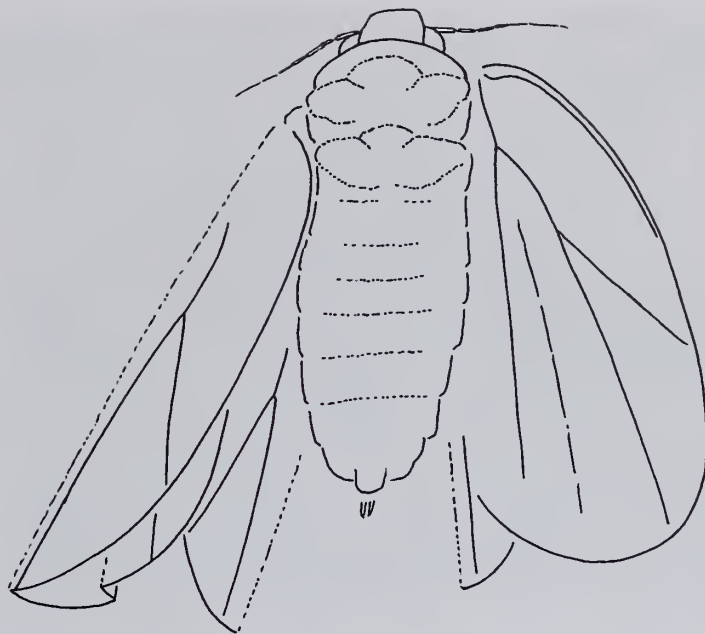

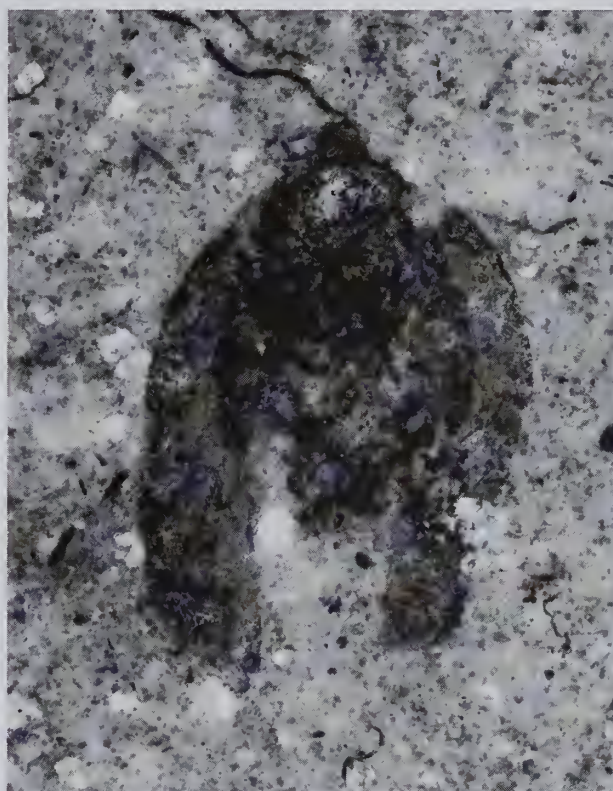Fig. 7 *Juleyrodes visnyai* sp. nov., holotype, habitus.

Fig. 8 *Juleyrodes* sp., male? PIN 2997/5071, Karatau.

herein; it has some eye and genital structures which cannot be interpreted at present, and probably some wax plates (preserved as shaded areas on the abdomen) (Fig. 9).

Genus *BURMOSELIS* gen. nov.

TYPE SPECIES. *Burmoselis evelynae* sp. nov.; probably Upper Cretaceous; Burmese amber.

NAME. From Burma (now Myanmar) and genus *Udamoselis*.

DESCRIPTION. Forewing widened towards obliquely rounded apex. Costal margin weakly arched. Rs about twice as long as the R stem. Nearly complete M starting slightly basad of R1 origin (just before

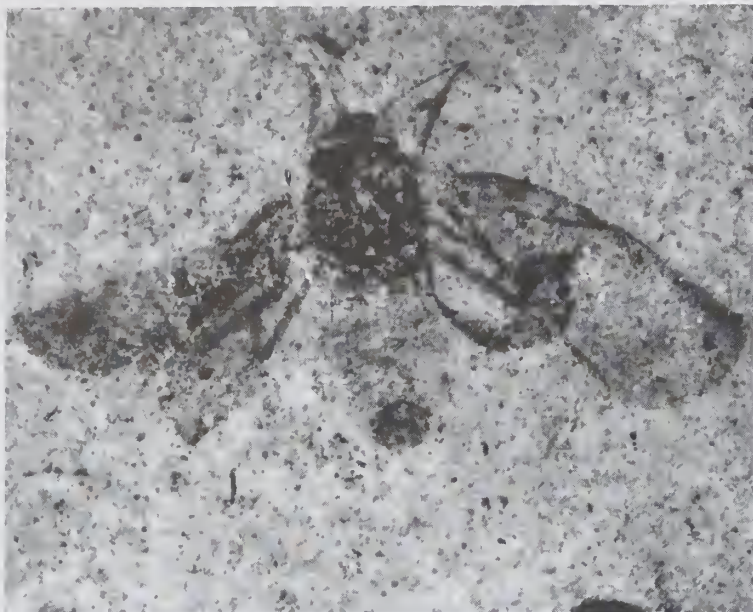Fig. 6 *Juleyrodes visnyai* sp. nov., holotype, female? PIN 2997/3837 (positive impression), Karatau.

Fig. 9 Bernaeinae gen. indet., male? PIN 2239/532, Karatau.

wing midlength), nearer to CuA distally. Anal vein occupying 1/3 of clavus. Head narrower than thorax. Antennae 11-segmented, flagellum slender. Basitarsus no longer than distitarsus. Ovipositor long.

OTHER SPECIES.   None.

REMARKS.   Similar to *Juleyrodes* and can be separated from Lebanese amber genera (including several undescribed ones) in the almost complete M nearer to CuA distally, narrower head and shorter basitarsus. Distinct from *Juleyrodes* in the shorter M and A, longer R stem, and less arched costal margin.

Burmoselis evelynae sp. nov.   Figs. 10, 11

HOLOTYPE.   NHM Palaeontol. Dept., In.20193, complete female near the edge of a large amber piece containing several insects, a spider and a mite (the whitefly near the spider); Burmese amber; probably Upper Cretaceous, Hukawng Valley, Myanmar (Burma) (see Zherikhin & Ross, this volume); the only specimen.

NAME.   After Dr Evelyna Danzig, an authority on aleyrodids and coccids.

DESCRIPTION.   Forewing 2.2 times as long as wide, slightly dusky, gradually widening towards obliquely rounded apex. Costal margin weakly and evenly arched; C slightly thickened proximally. R stem nearly straight, raised. R1 almost as long as R stem, originating at 0.44 wing length, straight, faint distally, strongly converging with C. Rs twice as long as the R stem. M traceable from just beyond R1 origin (not joining CuA), distally nearer to CuA. CuA fine convex, slightly bent against R1 origin, probably marking the end of M+CuA fusion (then M+CuA equal to R stem). Clavus occupying 2/3 of wing length; anal vein short, about 1/3 of clavus and 1/5 of wing length. Hindwing 2.4 times as long as wide, rounded apically, transparent; origin of indistinct R1 just beyond wing midlength. Body shrivelled. Head 3/4 as wide as the mesothorax, with anterior margin slightly biconvex and medially emarginate (indication of coronal suture, if not an artifact of preservation). Antenna 11-segmented, apices of flagellomeres marked with rhinaria; 1st flagellomere almost as long as three following combined; pedicel large, elongate, obliquely truncate apically. Rostrum invisible, but (judging from the size of a

Fig. 10 *Burmoselis evelynae* sp. nov., holotype, female NHM In.20193, Burmese amber.

large gas bubble enclosing it) possibly reaching hind coxae. Pronotum preserved almost in vertical plane. Legs moderately long, tibial setae not conspicuous (visible at least on fore tibiae). Basitarsus subequal to distitarsus in hind leg, and slightly shorter than it in other legs. Paronychium presumably small. Pregenital abdomen largely membranous (preserved markedly flattened dorsoventrally). Paired dark areas visible on five(?) abdominal segments, possibly representing wax plates. Ovipositor directed posteriorly, projecting beyond anal tube for about 1/2 length of the rest of abdomen, with 4 long lateral bristles on each side.

MEASUREMENTS   (mm). Forewing length, 1.1, its width, 0.5; hindwing length, 0.95, its width, 0.4; body length (including ovipositor), 0.95; mesothorax width, 0.28; antenna length, 0.3; estimated rostrum length, 0.3; fore tibia length, 0.23, fore tarsus length, 0.1; hind tibia length, 0.4, hind tarsus length, 0.18; projecting part of ovipositor, 0.2.

OTHER FOSSIL WHITEFLIES

Imagines

Middle Purbeck of England (Lower Cretaceous: Berriasian): a forewing of *Juleyrodes* sp. was recently found (D. Shcherbakov & R. Coram, pers. comm.).

Lebanese amber (Lower Cretaceous): whiteflies are exceptionally numerous, about 70% of homopterans, and 9% of all insects! (Poinar, 1992): *Bernaea neocomica, Heidea cretacica* (Schlee, 1970), and several undescribed genera, including the oldest member of Udamoselinae (D. Shcherbakov & D. Azar, pers. obs.).
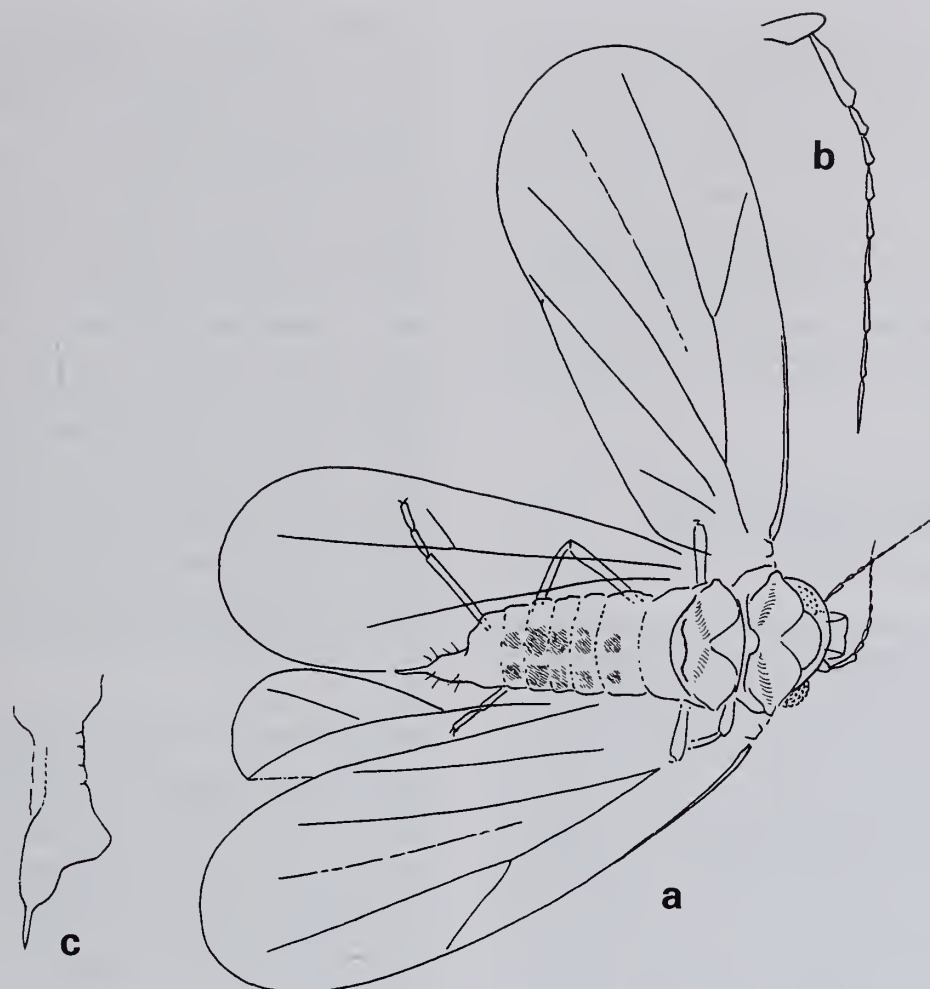
Fig. 11 *Burmoselis evelynae* sp. nov., holotype: (a) habitus, dorsal; (b) antenna, schematized, first segment not shown; (c) profile of abdomen.

Burmese amber: '*Aleurodicus' burmiticus* Cockerell, 1919, 1 male (Fig. 12). Schlee (1970: 32) doubted its assignment to Aleurodicinae, but the hindwing venation and genitalia confirm the subfamily placement (generic assignment doubtful).

Fig. 12 '*Aleurodicus' burmiticus* Cockerell, holotype, NHM In.19134, Burmese amber.

Baltic amber: '*Aleyrodes' aculeatus* Menge, 1856, 1 female? (holotype presumably destroyed), not figured, and diagnosed only as 'similar to living *A. chelidonii* Latr., except for the end of abdomen being acuminate and bearing two small pointed processes, which was found in both sexes by Burmeister (Entomol. II: 82)', so generic position is undeterminable. There are 15 aleyrodid specimens in Copenhagen collection (Larsson, 1978), partly studied but not named by Schlee (1970); 2 undescribed specimens in the PIN collection and 3 unstudied specimens (2 imagines, 1 pupa?) in the NHM (A. Ross, pers. comm.).

Whiteflies are also recorded in Mexican and Dominican amber (Poinar, 1992).

Nymphs

Purbeck and Wealden of England (Lower Cretaceous; Berriasian-Barremian): very small oval nymphs occur regularly (more rarely in Wealden), resembling pupal cases of Aleyrodoidea (Jarzembowski & Coram, 1997: figs. 6–8).

Lithographic Limestone of Montsech (Lower Cretaceous; Berriasian): pupal case of ?Bernaeinae incertae sedis (Whalley & Jarzembowski, 1985: figs 12–13).

Eocene (Isle of Wight): pupal case of Aleyrodoidea (Jarzembowski & Ross, 1993: fig. 2).

Pliocene (Hessen): *Aleurochiton petri* Rietschel, 1983, pupal case.

Taxa excluded from Aleyrodomorpha

Upper Permian: *Permaleurodes rotundatum* Becker-Migdisova, 1959 (South Siberia) and *Aleuronympha bibulla* Riek, 1974 (South Africa),

both nymphs, and assigned to a separate family Permaleurodidae Becker-Migdisova, 1959 in the Aleyrodoidea. The former genus was regarded by Evans (1963), Hennig (1969) and Schlee (1970) as a doubtful member of Aleyrodomorpha, and by Mound & Halsey (1978) even as a cockroach nymph. In fact both these nymphs belong to primitive Homoptera, most probably to Protopsyllidiidae or related group of Psyllinea.

Lower Cretaceous (Brazil): *Megaleurodes megocellata* Hamilton, 1990, ascribed to Aleyrodoidea and tentatively assigned to the Permian family Boreoscytidae. The genus is possibly based on a poorly preserved planthopper, and has nothing in common with boreoscytids (primitive group of Aphidinea).

AN OVERVIEW OF BURMESE AMBER HEMIPTERA

Of 1200 animal inclusions recorded in Burmese amber from NHM collection by A.P. Rasnitsyn, 75 are Homoptera and 9 Heteroptera, so Hemiptera totalling 84 specimens, or 7%, are in 6th place, after Isoptera and before Diplopoda. (It is the same percentage as for Dominican amber Hemiptera from the collection of Smithsonian Institution, identified by A.P. Rasnitsyn). More than half (47 specimens) are Cicadinea (=Auchenorrhyncha), dominated by the extant family Achilidae (Fulgoroidea; 27 specimens). Achilids, feeding on fungi and often corticolous, are numerous (but not dominating) in Baltic amber as well. Burmese amber achilids are represented by both nymphs (including exuvia) and imagines. Only two specimens are identified, both of '*Liburina*' *burmitina* Cockerell (erroneously assigned to the Delphacidae genus *Liburnia* Stål): the holotype, In.19105, and another specimen, In.20150(1). The holotype was reexamined and shows no metatibial spur, and the forewing venation is characteristic of Achilidae; to elucidate the generic position of the species, it should be compared to several extinct genera described from the Cretaceous and Baltic amber.

A second fulgoroid family, the extant Cixiidae, is represented by two imagines: *Plecophlebus nebulosus* Cockerell, holotype In.19094, and one specimen of another genus. *Plecophlebus* was described in Trichoptera, but later transferred to Fulgoroidea (Botosaneanu, 1981). A third, extinct fulgoroid family is of exceptional interest: 2 imagines of different genera belong to the group otherwise occurring in the Aptian of Mongolia and Cretaceous ambers of Taimyr and New Jersey (Shcherbakov, in prep.). 11 more planthopper imagines and nymphs are at present not determinable to family level. Total Fulgoroidea (42 specimens) constitute most of Cicadinea, like in Dominican amber. The only other auchenorrhynchous group determined is Cercopoidea (possibly Aphrophoridae, 1 imago), always rare in ambers. The remaining 4 specimens of Cicadinea are undeterminable.

Other Homoptera ('Sternorrhyncha') are represented with 19(?+1) coccids (males, females, and possibly nymphs) and 3 whiteflies: '*Aleurodicus*' *burmiticus* Cockerell, 1919 (Udamoselinae s.l.), holotype male In.19134, *Burmoselis evelynae* gen. et sp. nov. (Bernaeinae), holotype female In.20193a, and an undetermined aleyrodid, In.20703. Coexistence of Bernaeinae and Udamoselinae is otherwise known only in Early Cretaceous Lebanese amber. A further 5 specimens of Homoptera are indeterminable.

Six out of nine Heteroptera are Enicocephalidae (such an unusually high proportion is comparable only to that in Lebanese amber): *Disphaerocephalus constrictus* Cockerell, holotype In.19112; *D. macropterus* Cockerell, holotype In.19123(1); *Electrocephalus swinhoei* Cockerell, holotype In.19113; *Paenicotechys fossilis*

(Cockerell), holotype In.19095; Enicocephalidae indet. (2 specimens). Other families are Coreidae s.l. and Ochteridae, one specimen of each (Yu. A. Popov det.); one more specimen is tentatively determined as a heteropteran.

Psyllomorpha are very rare or absent in Cretaceous and Paleogene faunas, and Burmese amber is not an exception. However, two other homopteran groups, leafhoppers (Cicadellidae *s.l.*) and aphids, are surprisingly lacking from the fauna discussed. Aphids are abundant and diverse since the Early Cretaceous, and well represented in Taimyr, Canadian and Baltic ambers; however, they are very rare in Lebanese amber (unpubl. data), virtually absent from Dominican amber (only 2 specimens recorded; Heie & Poinar, 1988; Wegierek, 1998), and now mainly extratropical, so their absence from Burmese amber could be evidence of a tropical paleoclimate. Leafhoppers, likewise abundant since the Early Cretaceous in compression fossil faunas, are (in contrast to aphids) not yet recorded in Cretaceous ambers, well represented in all Cenozoic ambers, and are now diverse on all continents and large islands (including Australia and Madagascar). So their absence is more intriguing and may be due to taphonomical reasons.

REFERENCES

Becker-Migdisova E.E. 1959. Some new representatives of Sternorrhyncha from the Permian and Mesozoic of the USSR. *In, Materialy k 'Osnovam paleontologii'*, **3**: 104–116. Paleontologicheskii Institut Akademii Nauk SSSR: Moscow.

Bemis F.E. 1904. The aleyrodids, or mealy-winged flies, of California, with references to other American species. *Proceedings U. S. National Museum*, **27**: 471–537.

Bondar G. 1923. *Aleyrodideos do Brasil*. Imprensa Official do Estado: Bahia.

Börner C. 1904. Zur Systematik der Hexapoden. *Zoologischer Anzeiger*, **27**: 511–533.

——— 1910. Die Flügelgeaderung der Aphidina und Psyllina. *Zoologischer Anzeiger*, **36** (1): 16–24.

Botosaneanu L. 1981. On a false and a genuine caddis-fly from Burmese amber (Insecta: Trichoptera, Homoptera). *Bulletin Zoologisch Museum Universiteit van Amsterdam*, **8**: 73–78.

Byrne D.N., Buchmann S.L. & Spangler H.G. 1988. Relationship between wing loading, wingbeat frequency and body mass in homopterous insects. *Journal of Experimental Biology*, **135**: 9–23.

——— **& Hadley N.F.** 1988. Particulate surface waxes of whiteflies: morphology, composition and waxing behaviour. *Physiological Entomology*, **13**: 267–276.

Campbell B.C., Steffen-Campbell J.D. & Gill R.J. 1994. Evolutionary origin of whiteflies (Hemiptera: Sternorrhyncha: Aleyrodidae) inferred from 18S rDNA sequences. *Insect Molecular Biology*, **3** (2): 73–88.

———, ———, **Sorensen J.T., & Gill R.J.** 1995a. Paraphyly of Homoptera and Auchenorrhyncha inferred from 18S rDNA nucleotide sequences. *Systematic Entomology*, **20** (3): 175–194.

———, ——— **& Gill R.J.** 1995b. Origin and radiation of whiteflies: an initial molecular phylogenetic assessment. *In*, Gerling, D. & Mayer, R.T. (editors), *Bemisia: 1995 Taxonomy, biology, damage control and management*: 29–51. Intercept: Andover.

Carver M. 1991. Superfamily Aleyrodoidea. *In*, Naumann, I.D. (editor), *The insects of Australia*, 2nd ed.: 450–452. Melbourne Univ. Press: Carlton.

Cockerell T.D.A. 1919. Insects in Burmese amber. *Entomologist*, **52**: 241–243.

Dohlen C.D.von & Moran N.A. 1995. Molecular phylogeny of the Homoptera: a paraphyletic taxon. *Journal of Molecular Evolution*, **41**: 211–223.

Enderlein G. 1909. *Udamoselis*, eine neue Aleurodiden-Gattung. *Zoologischer Anzeiger*, **34**: 230–233.

Evans J.W. 1963. The phylogeny of the Homoptera. *Annual Review of Entomology*, **8**: 77–94.

Gill R.J. 1990. The morphology of whiteflies. In: D. Gerling (ed.). *Whiteflies: their bionomics, pest status and management*: 13–46. Intercept: Andover.

Gomez-Menor J. 1944. Aleirodidos de interes agricola. *Trabajos de Estacion Fitopatologica y Agricola Madrid*, Ser. Fitopatologica, **133**: 1–36.

Hamilton K.G.A. 1990. Homoptera. In, D.A. Grimaldi (ed.). Insects from the Santana Formation, Lower Cretaceous, of Brazil. *Bulletin of the American Museum of Natural History*, **195**: 82–122.

Haupt H. 1934. Neues über die Homoptera-Aleurodina. (Stellung im System, äussere Anatomie, Biologie, 2 neue Arten.) *Deutsche Entomologische Zeitschrift*, 1934: 127–141.

Heie O. & Poinar G.O., Jr. 1988. *Mindazerius dominicanus* nov. gen., nov. sp., a fossil aphid (Homoptera, Aphidoidea, Drepanosiphidae) from Dominican amber. *Psyche*, **95**: 153–165.

Hennig W. 1969. Die Stammesgeschichte der Insekten. *Senckenberg-Buch*, **49**. W.Kramer: Frankfurt am Main.

Jarzembowski E.A. & Coram R. 1997. New fossil insect records from the Purbeck of Dorset and the Wealden of the Weald. *Proceedings of the Dorset Natural History and Archaeological Society*, **118**: 119–124.

—— **& Ross A.** 1993. Time flies: the geological record of insects. *Geology Today*, Nov–Dec. 1993: 218–223.

Larsson S.G. 1978. Baltic amber – a palaeobiological study. *Entomonograph*, **1**. Scandinavian Science Press: Klampenborg.

Menge A. 1856. Lebenszeichen vorweltlicher, im bernstein eingeschlossener thiere. In: *Programm, . . . öffentlichen Prüfung der Schüler der Petrischule*, pp. 1–32. A.W. Kafemann: Danzig.

Mound L.A. & Halsey S.H. 1978. *Whitefly of the world. A systematic catalogue of the Aleyrodidae (Homoptera) with host plant and natural enemy data*. British Museum (Natural History) & J. Wiley: Chichester.

Navone P. 1987. Origine, struttura e funzioni di escreti e secreti entomatici di aspetto ceroso distribuiti sul corpo mediante zampe. *Anni di Facolti di Sciencia Agraria dell'Università di Torino*, **14**: 237–294.

Poinar G.O., Jr. 1992. *Life in amber*. Stanford University Press: Stanford.

Quaintance A.L. & Baker A.C. 1913. Classification of the Aleyrodidae. Part I. *Technical Series, Bureau of Entomology, U. S. Department of Agriculture*, **27**(1): 1–93.

—— & —— 1914. Classification of the Aleyrodidae. Part II. *Technical Series, Bureau of Entomology, U. S. Department of Agriculture*, **27** (2): 95–109.

Riek E.F. 1974. An unusual immature insect from the Upper Permian of Natal. *Annals of Natal Museum*, **22** (1): 271–274.

Rietschel S. 1983. *Aleurochiton petri* n. sp., eine Mottenschildlaus (Homoptera, Aleyrodina) aus dem Pliozän von Neu-Isenburg, Hessen. *Carolinea*, **41**: 97–100.

Sampson W.W. 1943. A generic synopsis of the hemipterous superfamily Aleyrodoidea. *Entomologica Americana*, **23** (3): 173–223.

—— **& Drews E.A.** 1957. Keys to the genera of the Aleyrodinae and notes on certain genera (Homoptera: Aleyrodinae). *Annals and Magazine of Natural History*, **9**: 689–697.

Schlee D. 1969. Sperma–Übertragung (und andere Merkmale) in ihrer Bedeutung für das phylogenetische System der Sternorrhyncha (Insecta, Hemiptera). Phylogenetische Studien an Hemiptera. I. Psylliformes (Psyllina and Aleyrodina) als monophyletische Gruppe. *Zeitschrift für Morphologie der Tiere*, **64**: 95–138.

—— 1970. Verwandtschaftsforschung an fossilen und rezenten Aleyrodina (Insecta, Hemiptera). *Stuttgarter Beiträge zur Naturkunde*, **213**: 1–72.

Shcherbakov D.E. 1990. Extinct four-winged ancestors of scale insects (Homoptera: Sternorrhyncha). *Proceedings of the 6th International Symposium of Scale Insect Studies*, Cracow, II: 23–29.

—— 1996. Origin and evolution of the Auchenorrhyncha as shown by the fossil record. In C.W. Schaefer (ed.). *Studies on Hemipteran Phylogeny*: 31–45. Entomological Society of America: Lanham (Thomas Say Publications in Entomology: Proceedings).

Solomon M.E. 1935. On a new genus and two new species of Western Australian Aleyrodidae. *Journal and Proceedings of the Royal Society of Western Australia*, **21**: 75–91.

Szelegiewicz H. 1971. Cechy autapomorficzne w budowie skrydel Sternorrhyncha (Hemiptera) i ich znaczenie dla oceny paleozoicznych przedstawicieli tej grupy pluskwiakow. *Annales Zoologici*, **29** (2): 15–81. [English translation 1976, National Center for Scientific, Technical and Economic Information: Warsaw.]

Visnya A. 1941. A gigantic species of Aleurodidae (Homoptera) from greenhouse-orchideas. *Folia Entomologica Hungarica*, **6** (1/2): 4–15.

Weber H. 1935. Der Bau der Imago der Aleurodinen. Ein Beitrag zur vergleichenden Morphologie des Insektenkörpers. *Zoologica (Stuttgart)*, **33**: 1–71.

Wegierek P. 1998. Fossil representatives of the family Greenideidae (Hemiptera, Aphidoidea). *First Paleoentomological Conference*, 1998, Abstracts: 47. Moscow: Paleontological Institute of the Russian Academy of Sciences.

Whalley, P.E.S. & Jarzembowski, E.A. 1985. Fossil insects from the Lithographic Limestone of Montsech (late Jurassic-early Cretaceous), Lérida Province, Spain. *Bulletin of the British Museum of Natural History (Geology)*, **38** (5): 381–412.

Wootton R.J. & Newman D.J.S. 1979. Whitefly have the highest contraction frequencies yet recorded in non-fibrillar flight muscles. *Nature*, **280**: 402–403.

Zherikhin V.V. 1980. Class Insecta. In: *Razvitie i smena bespozvonochnyh na rubezhe mezozoya i kainozoya*: 40–97. Nauka: Moscow.